



Magnetoreception and magnetic navigation in fishes: a half century of discovery

Lewis C. Naisbett-Jones¹ · Kenneth J. Lohmann¹

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Abstract

As the largest and most diverse vertebrate group on the planet, fishes have evolved an impressive array of sensory abilities to overcome the challenges associated with navigating the aquatic realm. Among these, the ability to detect Earth's magnetic field, or magnetoreception, is phylogenetically widespread and used by fish to guide movements over a wide range of spatial scales ranging from local movements to transoceanic migrations. A proliferation of recent studies, particularly in salmonids, has revealed that fish can exploit Earth's magnetic field not only as a source of directional information for maintaining consistent headings, but also as a kind of map for determining location at sea and for returning to natal areas. Despite significant advances, much about magnetoreception in fishes remains enigmatic. How fish detect magnetic fields remains unknown and our understanding of the evolutionary origins of vertebrate magnetoreception would benefit greatly from studies that include a wider array of fish taxa. The rich diversity of life-history characteristics that fishes exhibit, the wide variety of environments they inhabit, and their suitability for manipulative studies, make fishes promising subjects for magnetoreception studies.

Keywords Map · Compass · Orientation · Migration · Homing

Introduction

Aquatic environments are among the most challenging habitats on the planet for navigation. Animals migrating underwater confront a world in which visual cues are often limited or absent, while currents continuously displace swimming animals from their paths. Despite the inherent difficulties of navigating in the aquatic realm, numerous fishes routinely complete astonishing long-distance journeys. Among these are (1) the transoceanic migrations of great white sharks (*Carcharodon carcharias*), which travel some 10,000 km between Australian and South African waters (Bonfil et al. 2005); (2) the homing of Pacific salmon (*Oncorhynchus* sp.) to their natal rivers from oceanic feeding grounds in the Pacific after a multi-year absence (Quinn 2018); and (3) the seasonal reproductive migrations of bluefin tuna (*Thunnus thynnus*) between feeding areas in the Atlantic Ocean and

spawning grounds, either in the Gulf of Mexico or the Mediterranean Sea (Block 2001; Aranda et al. 2013).

Fishes and other long-distance marine migrants exploit a variety of sensory cues to guide their movements, including visual, auditory, and olfactory cues, as well as cues from waves and water movements (Lohmann et al. 2008a). An additional source of information, present in all environments that fish inhabit, is Earth's magnetic field. The first investigations into whether fish might sense the geomagnetic field were conducted in the early 1970s (Branover et al. 1971; Rommel and McCleave 1973). The work was inspired, in part, by reports of magnetic sensitivity in several invertebrates (e.g., Brown et al. 1960; Becker 1964) and the discovery of a magnetic compass sense in birds (Wiltschko and Merkel 1966). A half century later, phylogenetically diverse fish are now known to detect Earth's magnetic field and use it to guide movements over a variety of spatial scales. The last decade in particular has seen a substantial increase in the number of publications related to fish magnetoreception (Fig. 1) and has highlighted the need for a synthesis of the literature. Here we review the evidence for magnetoreception in fishes since the establishment of the field 50 years ago. We begin with a brief description of Earth's magnetic field and the characteristics that make it useful

This paper is dedicated to the memory of Prof. David L. Noakes.

✉ Lewis C. Naisbett-Jones
lnaisbettjones@gmail.com

¹ Department of Biology, University of North Carolina, Chapel Hill, NC 27599, USA

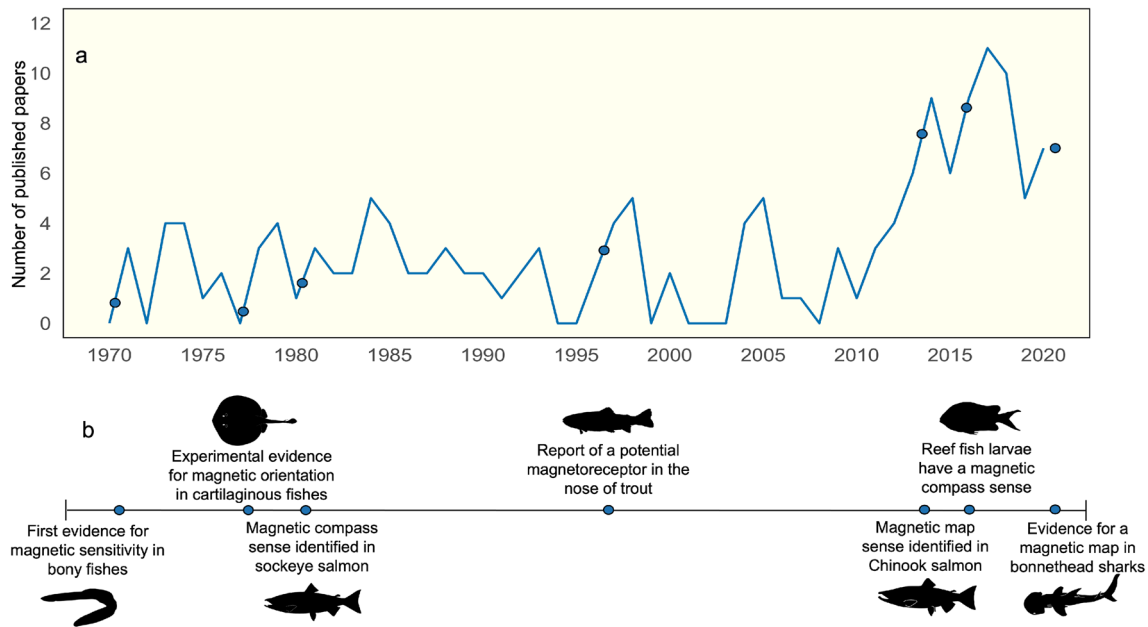


Fig. 1 **a** The number of published papers investigating magnetoreception in fishes since the first paper on the subject in 1971 (survey goes through 2020). **b** Timeline of some significant advances. Silhouette

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in navigation. We then describe approaches to investigating magnetoreception in fishes and summarize the evidence for magnetoreception in the two largest groups of fishes, the bony fishes and the cartilaginous fishes. Finally, we discuss possible mechanism(s) of magnetic field detection in fishes, highlight groups that have not yet been studied in the context of magnetoreception, and conclude by discussing how future work on fishes is likely to expand the horizons of magnetoreception research.

Properties of Earth's magnetic field

Earth's magnetic field represents an extremely reliable, omnipresent sensory cue. It is present during all times of day and exists at all locations on the planet, from the depths of the ocean to the uppermost part of the atmosphere. Thus, the geomagnetic field is present throughout the aquatic realm, making it arguably the most pervasive cue available to fishes and other aquatic animals. The ubiquity of the geomagnetic field might be the principal reason why diverse aquatic animals have evolved the ability to use it in orientation, including molluscs (Cain et al. 2005), crustaceans (Lohmann et al. 1995; Ugolini and Pezzani 1995; Lohmann and Ernst 2013), sea turtles (Lohmann et al. 2012) and diverse fishes. In this section, we provide a brief overview of the geomagnetic field (Fig. 2a) focusing on the properties that make it useful for animal navigation.

Animals can extract two types of information from the geomagnetic field: (1) directional, or “compass” information; and (2) positional or “map” information. Animals with a magnetic compass sense use the direction of magnetic field lines to maintain a consistent heading in a particular direction such as north or south (Lohmann 2010). By contrast, animals with a magnetic map sense rely on regular spatial features of the geomagnetic field to derive positional information, in effect using the field to determine where they are (Lohmann et al. 2007). Several geomagnetic field elements vary predictably across the surface of the earth (Skiles 1985; Fig. 2b). Two of these parameters, inclination angle and total intensity, vary in different directions over much of the globe, so that the two form a large-scale bi-coordinate grid over many oceanic regions (Lohmann et al. 1999, 2007). Evidence indicates that several fishes, as well as sea turtles and possibly other animals, exploit this pattern of magnetic variation as a kind of magnetic map (Lohmann et al. 2007, 2012; Putman et al. 2014c; Naisbett-Jones et al. 2017; Keller et al. 2021).

In addition to these global patterns of magnetic variation, concentrations of magnetic minerals in Earth's crust create additional, localized magnetic spatial patterns that animals might, in some cases, use in orientation and navigation. These finer-scale variations (or anomalies) in magnetic topography are far more complex than Earth's main dipole field. Although these localized anomalies typically only account for less than 1% of the total magnetic field, the gradients associated with anomalies can be significant and they

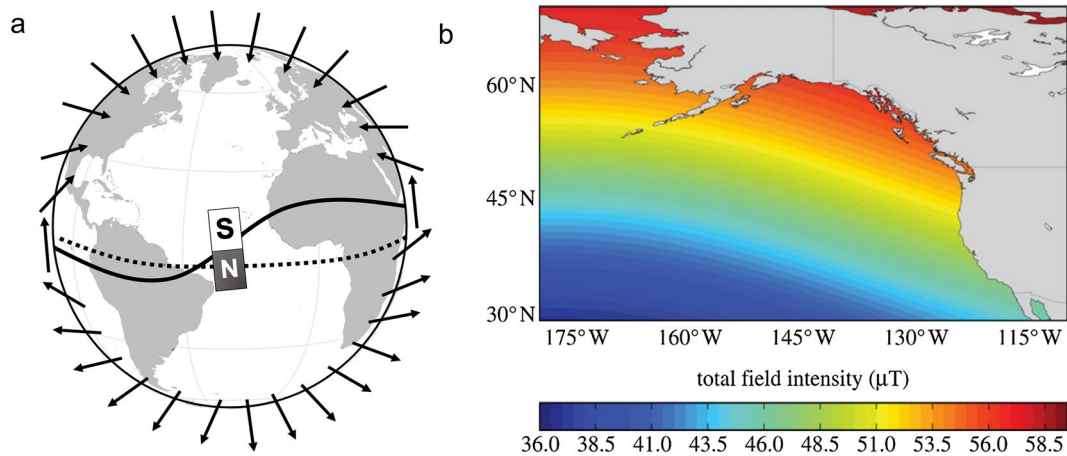


Fig. 2 Diagrammatic representation of the earth's magnetic field. **a** On a global scale, the geomagnetic field resembles the dipole field of a giant bar magnet (the north pole of the hypothetical magnet is directed toward the southern hemisphere). Magnetic field lines (represented by arrows) intersect the earth's surface in a predictable way across the globe. At the magnetic equator (solid curving black line) field lines are parallel to the earth's surface and the inclination angle is zero; at the poles field lines are perpendicular to the earth's sur-

face and the inclination angle is 90 degrees. Dotted curved line represents the geographic equator. **b** Map of the western North Pacific. Like inclination angle, the magnetic field intensity also varies across earth's surface but in a slightly different direction than does inclination angle; thus, different geographic areas have different magnetic signatures consisting of specific combinations of inclination and intensity (Modified from Putman et al. 2014a). A more detailed descriptions of the geomagnetic field is provided by Skiles (1985)

can create distinctive magnetic patterns (McElhinny and McFadden 1999). For instance, at the ocean-basin scale, seafloor spreading creates somewhat linear magnetic hills and valleys that run parallel to mid-ocean ridges; this magnetic topography has been proposed to be used by some marine migrants (Klinowska 1985; Kirschvink et al. 1986; Walker et al. 1992). Geological formations such as seamounts also have unique magnetic properties which might make them useful as navigational landmarks for fishes and other marine animals; for example, scalloped hammerhead sharks (*Sphyrna lewini*) have been proposed to navigate using local, fine-scale magnetic anomalies associated with seamounts and the sea floor (Klimley 1993).

Methods of studying responses of fishes to magnetic fields

Observational studies, such as tracking fish through the wild and determining migratory paths, can provide a useful starting point for considering the navigational cues that might be available en route. Studies of this nature are especially valuable for organisms that are too large for laboratory-based experiments. In some cases, analysis of movement trajectories has provided valuable insight into cues that might underlie navigation (Klimley 1993; Alerstam et al. 2001; Azumaya et al. 2016). Because animals in their natural habitat usually have access to numerous sensory cues, however, inferring which are used to guide an animal along a given path is often challenging (Lohmann et al. 2008a).

Compelling evidence that an animal can detect a given sensory cue can often be acquired from experiments in which the cue is manipulated in some way and a response of the animal to the altered cue is observed. In the case of magnetoreception, altering magnetic fields has traditionally been achieved using two main approaches, each of which has advantages and limitations. Studies using various types of electromagnetic coil systems to carefully control magnetic field conditions have provided the strongest and most direct experimental evidence for magnetoreception in fishes and other animals (Wiltschko and Wiltschko 1995). While a number of magnetic coil configurations exist, they each serve the same purpose in behavioral experiments: to enable researchers to expose animals to carefully controlled magnetic fields, which often resemble the natural magnetic field of the earth.

In most studies, magnetic coil systems have been used to control the ambient field throughout an arena where an animal moves. If coils are miniaturized, however, then they can be placed on animals to alter the magnetic field in a small part of the body (Walcott and Green 1974). In one field study with salmon (Yano et al. 1997), small magnetic coils placed on the heads of fish were used in an attempt to disrupt the ability of fish to sense magnetic fields in the natural environment. No clear effects of the coils were observed, but the small sample size ($n=4$) and availability of multiple cues in the environment make interpretation of the results difficult. To our knowledge, such studies have not been attempted with other fishes, likely due to logistical constraints; for example, most species lack a hard external surface to which

devices can be attached and many fishes move over long distances, making it difficult to monitor movements.

An alternative approach to changing the ambient field with magnetic coil systems is to change it with magnets. Although simpler, the technique of using magnets is not without caveats. Magnets typically generate magnetic fields that are significantly stronger than earth strength; they also generate steep magnetic field gradients that do not exist in nature. For these reasons, results of studies in which animals are exposed to magnets can sometimes be difficult to interpret. Nevertheless, magnets have proven to be a useful tool for demonstrating sensitivity of fishes to magnetic cues under some conditions (e.g., Newton and Kajiura 2017).

Quantifying magnetic orientation behavior

Determining how an animal orients in response to different magnetic field conditions is a key element of most magnetic behavioral experiments. Normally, animals are released within arenas and their directional tendencies are recorded. While this might at first glance appear to be a simple and straightforward task, it can be quite challenging. A set of experimental conditions must be created that results in clear responses. The researchers must then determine how to systematically quantify the behavior, a problem compounded when it is difficult to predict how an animal is going to behave. Indeed, even the responses of a single individual to the same stimulus can vary depending on the animal's behavioral state at the time of testing (e.g., whether it is motivated to mate, migrate, or forage), its health, and what other cues are available.

These considerations make behavioral investigations into any sensory modality challenging, but when magnetic fields are involved, the situation becomes even more difficult. Accumulating evidence suggests that the use of magnetic cues is likely restricted to certain behavioral scenarios; in addition, the magnetic sense may be inherently noisy, so that some degree of temporal averaging is required for the processing of magnetic cues (Wiltschko and Wiltschko 1991; Johnsen et al. 2020). Researchers can increase the likelihood of acquiring meaningful behavioral data by choosing test species that adapt readily to the conditions of laboratory studies. In fishes, favorable traits include high physiological tolerance to abiotic parameters (e.g. temperature, salinity, and dissolved oxygen levels) and solitary (non-schooling) behavior that allows testing of individuals in isolation. Odds of success may also be improved by testing fish at or near life-history stages in which oriented movements are critical for survival (e.g., Putman et al. 2014c; Naisbett-Jones et al. 2017; O'Connor and Muheim, 2017), although the discovery that some fish spontaneously align with the magnetic field (e.g., Kalmijn 1978; Hart et al. 2012) suggests that at

least some species use magnetic information continuously throughout their lives.

Another factor that makes behavioral experiments on magnetic orientation challenging with fishes is that no universal testing apparatus exists, in part because different species move in diverse ways that often change through ontogeny. For example, modes of locomotion include the sinuous, lateral waves of anguilliform swimming characteristic of eels (Wootton 1990), the slow-moving “benthic walking” behavior of flatfish (Fox et al. 2018) and the continuous swimming of some sharks and bony fishes that are obligate ram ventilators (Roberts 1975). Each of these locomotory modes poses different challenges for researchers attempting to monitor orientation behavior. As a result, a number of different experimental arenas have been designed, ranging from simple circular arenas (Putman et al. 2014c) to more elaborate arenas and mazes (Nishi et al. 2018; Newton and Kajiura 2020a). The need to develop an arena that matches the behavior of each species of fish—and sometimes each life-history stage—stands in sharp contrast to magnetic orientation studies with birds, most of which rely on a standard experimental arena that takes advantage of the migratory restlessness characteristic of many songbirds (Emlen and Emlen 1966; Wiltschko and Wiltschko 1995).

Evidence for magnetoreception in fishes

Despite the challenges associated with testing behavioral responses to magnetic fields, considerable evidence for magnetoreception has accumulated in fishes, especially in two main groups: the bony fishes (Osteichthyes) and the cartilaginous fishes (Chondrichthyes). In this section, we summarize evidence for magnetoreception derived from diverse approaches, including experiments focusing on magnetic compass orientation, experiments investigating the use of magnetic maps, studies of spontaneous alignment with the ambient magnetic field, studies using conditioning techniques, and correlative studies relating fish movements to magnetic field parameters.

Magnetoreception in bony fishes

Salmon (Salmonidae)

In the family *Salmonidae*, research has primarily focused on Pacific salmon from the genus *Oncorhynchus* and, to a lesser extent, salmon from the genus *Salmo*, which includes the Atlantic salmon *Salmo salar* (Table 1.). Although non-migratory forms of many salmon exist, the majority are anadromous; in other words, they migrate from freshwater

habitats where they hatch, to distant ocean foraging grounds, before returning to their natal streams to spawn and die (Quinn 2018). For these reasons, salmon have long been popular subjects for studies on the sensory basis of navigation in fishes. Indeed, they have shaped much of the current understanding of magnetoreception in fishes today.

Quinn (1980) reported the first unequivocal evidence for a magnetic compass sense in a fish. Sockeye salmon fry (*Oncorhynchus nerka*) from two populations were collected during their freshwater phase as they migrated from the gravel beds in which they hatched to the lakes where they feed and grow. Fish were released in an orientation arena and could exit through one of four equally spaced arms around the perimeter. The directions chosen by the young salmon were consistent with the hypothesis that they were orienting towards their respective lake habitats. Rotating the horizontal component of the ambient magnetic field by 90° resulted in a corresponding shift in the directional preference of the salmon fry, demonstrating that the orientation was based on magnetoreception. At night, the orientation persisted regardless of whether external celestial cues were occluded. During the day, magnetic compass orientation was only observed under conditions in which the fish were deprived of celestial cues. Thus, the results were consistent with the interpretation that celestial cues take precedence over magnetic cues during daytime migrations in sockeye salmon. Interestingly, during a subsequent study in which a different type of arena was used and night-time celestial cues were again occluded, salmon displayed bimodal magnetic orientation instead of orienting in a single direction as they had previously (Quinn and Brannon 1982). Although the reason for the different outcomes is unclear, one possibility is that the different arenas used in the two studies might have affected the responses of the fish (Quinn and Brannon 1982).

Evidence exists for two different functional types of magnetic compasses in animals. Some animals rely on the polarity of the horizontal component of the geomagnetic field to determine the direction of magnetic north, in much the same way that a human compass does (Lohmann et al. 1995; Kimchi and Terkel 2001). Other animals, however, possess a magnetic compass that relies in part on the inclination of the field (Wiltschko and Wiltschko 1972; Light et al. 1993). An animal with an inclination compass defines ‘poleward’ as the direction along the earth’s surface in which the angle formed between the total field vector and the gravity vector is smallest (Wiltschko and Wiltschko 1972). The diagnostic test for determining whether an animal possesses a compass based on the polarity or inclination of the magnetic field involves exposing animals to a field with an inverted vertical component and observing the response. To an animal with an inclination compass, such a field is reversed relative to the normal condition, but to an animal with a polarity compass, the two fields are the same (Wiltschko et al. 1993).

As a first step toward investigating the nature of the magnetic compass in fishes, Quinn et al. (1981) exposed sockeye salmon fry to a local magnetic field and a magnetic field in which the vertical component was inverted. Fish tested under the two magnetic fields oriented in similar directions. Thus, the results suggest that salmon have a polarity compass, although further investigations using additional fields, such as those used with birds and turtles (Wiltschko and Wiltschko 1972; Light et al. 1993), are needed to confirm these results.

The open-ocean migrations of young salmon likely involve complex navigational processes that function to guide the fish to appropriate oceanic feeding areas. The discovery that young sea turtles inherit a magnetic map in which regional magnetic fields elicit changes in swimming direction at crucial points in the migration (Lohmann 2001; Lohmann et al. 2012) stimulated a search for a similar navigational system in young fish. Juvenile Chinook salmon that had never been in the ocean were exposed to magnetic fields that exist at the northern and southern edges of their oceanic range, as well as to the unaltered ambient magnetic field of the test site in Oregon, USA (Putman et al. 2014c). Fish tested in the northern magnetic field oriented south, whereas fish tested in the southern magnetic field oriented north. In contrast, fish tested in the ambient magnetic field did not show a directional preference. The results indicate that young salmon derive positional information from Earth’s magnetic field and thus have a magnetic map sense. The magnetic map appears to help fish remain within favourable ocean habitats and offers a possible mechanism by which stocks might segregate into broad oceanic areas (Putman et al. 2014c). Because these experiments were performed on fish that had never migrated and thus had no opportunity to learn about how magnetic fields vary in the ocean, the results imply that the responses of the fish to regional magnetic fields are largely inherited (Putman et al. 2014c).

To investigate the magnetic field parameters involved in this inherited magnetic map, salmon were further tested under two magnetic field conditions designed to determine whether they relied on magnetic field intensity alone, inclination angle alone, or a combination of the two (Putman et al. 2014c). Specifically, the intensity of the northern magnetic field was paired with the inclination angle of the southern magnetic field, and vice versa. If the fish rely exclusively on intensity or inclination angle, then a response to one of these parameters should dictate in each case whether salmon perceive themselves to be north or south of their oceanic range. Instead, fish tested in either of these hybrid magnetic conditions oriented randomly, indicating that neither field intensity alone nor inclination angle alone is sufficient to determine position. Thus, the findings are consistent with the interpretation that salmon rely on combinations of magnetic field intensity and inclination angle to assess their position,

Table 1 Experimentally demonstrated behavioral responses of bony fishes to magnetic stimuli

Class	Order	Family	Species	Citations	Types of responses
Actinopterygii	Anguilliformes	Anguillidae	<i>A. anguilla</i>	(Branover et al. 1971; Tesch and Lelek 1973; Tesch 1974; Karlsson 1985; Tesch et al. 1992; Durif et al. 2013; Naisbett-Jones et al. 2017; Cresci et al. 2017b, 2019a)	Map, compass, Alignment, other
”	”	”	<i>A. japonica</i>	(Nishi et al. 2004, 2005, 2018; Nishi and Kawamura 2005)	Anomalous
”	”	”	<i>A. rostrata</i>	(McCleave et al. 1971; Rommel and McCleave 1973; Zimmerman and McCleave 1975; Souza et al. 1988)	Anomalous, conditioning, other
”	Salmoniformes	Salmonidae	<i>O. nerka</i>	(Quinn 1980; Quinn et al. 1981; Quinn and Brannon 1982)	Compass, other
”	”	”	<i>S. salar</i>	(McCleave et al. 1971; Rommel and McCleave 1973; Varanelli and McCleave 1974; Scanlan et al. 2018; Minkoff et al. 2020)	Map, conditioning, other
”	”	”	<i>S. trutta</i>	(Formicki et al. 1997, 2004)	Anomalous, alignment
”	”	”	<i>O. gorbusha</i>	(Putman et al. 2020)	Map
”	”	”	<i>O. keta</i>	(Quinn and Groot 1983)	Other
”	”	”	<i>O. mykiss</i>	(Chew and Brown 1989; Walker et al. 1997; Formicki et al. 1997; Haugh and Walker 1998; Hellinger and Hoffmann 2009, 2012; Putman et al. 2014b; Fitak et al. 2017, 2020)	Conditioning, anomalous, map, alignment
”	”	”	<i>O. tshawytscha</i>	(Taylor 1986; Putman et al. 2014c, 2018; Naisbett-Jones et al. 2020)	Anomalous, other, compass, map
”	Scombriformes	Scombridae	<i>T. albacares</i>	(Walker 1984)	Conditioning
”	Cypriniformes	Cyprinidae	<i>D. rerio</i>	(Shcherbakov et al. 2005; Takebe et al. 2012; Osipova et al. 2016; Krylov et al. 2016; Cresci et al. 2017a, 2018; Myklatun et al. 2018)	Conditioning, other, alignment, compass
”	”	”	<i>R. rutilus</i>	(Krylov et al. 2016)	Compass
”	”	”	<i>C. auratus</i>	(Becker 1974)	Other
”	”	”	<i>C. carpio</i>	(Hart et al. 2012)	Alignment
”	Beloniformes	Adrianichthyidae	<i>O. latipes</i>	(Myklatun et al. 2018)	Other
”	Kurtiformes	Apogonidae	<i>O. doederleini</i>	(Bottesch et al. 2016)	Compass
”	Perciformes	Pomacentridae	<i>C. atripectoralis</i>	(O’Connor and Muheim 2017)	Compass
”	Cichliformes	Cichlidae	<i>O. mossambicus</i>	(Shcherbakov et al. 2005)	Conditioning
”	Gadiformes	Gadidae	<i>M. aeglefinus</i>	(Cresci et al. 2019b)	Compass
”	Siluriformes	Siluridae	<i>K. vitreolus</i>	(Hunt et al. 2021)	Other

Compass = evidence that fishes use directional information in Earth’s magnetic field; map = evidence that fishes use positional information in Earth’s magnetic field; alignment = studies indicating spontaneous alignment of fishes relative to the axis of magnetic field lines; anomalous = avoidance, attraction, or other responses of fishes to strong (greater than earth strength) anomalous magnetic fields produced by a magnet, solenoid, or magnetic coil; conditioning = conditioning of fishes to magnetic field stimuli; other = other evidence (not included in the previous categories) that suggests or demonstrates magnetic sensitivity.

as other ocean migrants such as sea turtles and lobsters also appear to do (Boles and Lohmann 2003; Lohmann et al. 2004, 2012).

Magnetic maps have now been demonstrated in a number of salmon species, suggesting that an ability to derive

positional information from Earth’s magnetic field is widespread among the family *Salmonidae* (Putman et al. 2014b, 2020; Scanlan et al. 2018; Minkoff et al. 2020). A study on pink salmon (*Oncorhynchus gorbusha*) provides an interesting example of how positional information from Earth’s

magnetic field might be used during oceanic migrations (Putman et al. 2020). Young pink salmon that had never migrated were tested in two magnetic fields that exist at locations where the orientation adopted by the fish might indicate whether they were homing, orienting to the center of their range, or following their migratory route (Fig. 3a). In both cases, the observed orientation of the fish matched the direction fish would be expected to adopt if they were following their migratory route (Fig. 3b). These findings suggest that magnetic maps in young salmon, like those in young sea turtles (Lohmann et al. 2012), appear to be fine-tuned to the migratory routes of individual populations; in effect, the animals seem to inherit instructions that tell them what direction to swim when they encounter specific magnetic fields along a migratory pathway.

Another interesting aspect of these ‘inherited magnetic maps’ is that young fish and turtles both responded to magnetic fields that they would likely not encounter until months (or for turtles, even years) after first entering the sea. These results suggest that such maps, which are present before the animals migrate, are likely retained throughout an animal’s

early life; nevertheless, it is also possible that the responses are modified through experience and/or provide the framework upon which more expansive learned maps are constructed as an animal gains experience with its magnetic environment (Putman et al. 2017; Lohmann et al. this issue). Given that most salmon migrate to the ocean only once and to areas they have not previously been, an innate navigation system that guides the initial migration appears advantageous (Putman et al. 2020). Determining how magnetic maps change at different life-history stages of salmon, if indeed they do, remains an outstanding research challenge, one that is complicated by an incomplete understanding of the ocean migrations of many species.

In principle, salmon might use magnetic map information not only to navigate along open-sea migratory pathways, but also to help them return to their area of origin as adults (Quinn 1984). Indeed, recent findings provide evidence that young salmon, as well as young sea turtles, imprint on the magnetic field that exists in or near their area of origin and use this information to return to the natal area to reproduce (Lohmann et al. 2008b; Bracis and Anderson 2012; Putman

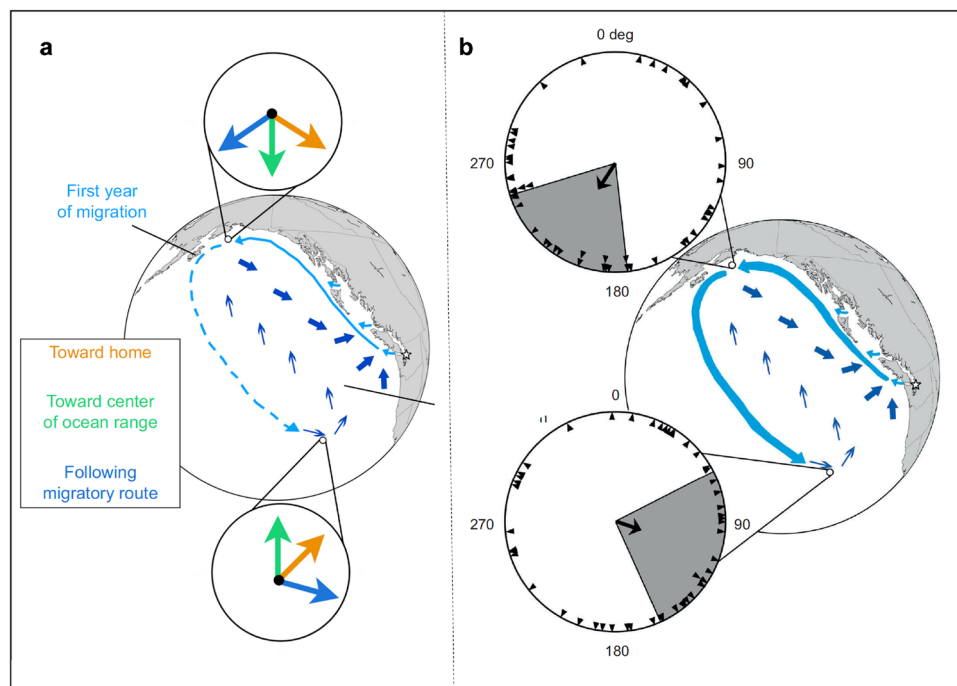


Fig. 3 Hypothesized and observed orientation responses of juvenile pink salmon to magnetic map information. **a** The migratory route of pink salmon and possible orientation responses of juvenile fish to magnetic map information. Light blue arrows show the migratory movements for the first year at sea (solid line=spring/summer, dashed line=autumn/winter). Dark blue arrows indicate the hypothesized movements during the second year in the ocean (thin arrows=movements during second spring/summer; thick arrows=homeward migrations in the second summer/autumn). Arrows within the circles show the direction that salmon might

adopt if they use magnetic cues to assess their location and orient. **b** Circular graphs show the orientation of juvenile pink salmon to magnetic fields that exist at the northern and southern ends of their migratory route. The orientation of pink salmon tested in the northern and southern magnetic fields differed significantly, indicating that they distinguished between the two magnetic fields and responded by swimming in different directions. Triangles represent the mean heading of individuals and the central arrow and gray shading shows the population-level mean direction and 95% CI, respectively (modified from Putman et al. 2020)

et al. 2013). For salmon, geomagnetic imprinting might occur in parallel with olfactory imprinting (Lohmann et al. 2008b); thus, magnetic cues might bring fish back into the general area of a river mouth, close enough for chemical cues to guide fish to the final destination.

A novel analysis of fisheries data has provided strong circumstantial evidence that young salmon do indeed imprint on the magnetic field of their home area, and that magnetic navigation plays a role in natal homing (Putman et al. 2013). The analysis exploited the fact that Earth's magnetic field changes gradually over time and that isolines of inclination and intensity shift slightly each year (Skiles 1985; Lohmann et al. 1999). Thus, the inclination and/or intensity existing at a particular location 1 year might drift northward the next year and possibly southward the year after that. Putman et al. (2013) examined how such variation influenced the homing migration of sockeye salmon that originated in the Fraser River of British Columbia, Canada. These fish typically spend two years at sea before making their homeward migration. To reach the mouth of the Fraser River from their open-ocean habitat, returning fish must detour around Vancouver Island to reach the river through one of two pathways, one of which lies to the north of the island and the other to the south. The existence of a long-term data set on the year-by-year proportion of salmon that used the northern or southern route provided a unique opportunity to test a central tenet of the imprinting hypothesis. If salmon imprint on the magnetic field of the area where they first enter the sea, then the number of fish that choose one route over the other might be influenced by subtle changes in Earth's magnetic field near Vancouver Island. Specifically, the route chosen by any given individual may depend on how closely the magnetic field at the entry to each passage resembles the magnetic field that the fish imprinted upon 2 years before when departing from the river.

Consistent with these predictions, analyses revealed that, when the magnetic intensity at the southern passage closely matched the field that existed at the mouth of the Fraser River when the fish departed, a greater proportion of salmon used the southern passage to return. Likewise, when the magnetic field intensity of the northern entryway closely matched what existed at the mouth of the Fraser River when the fish began their migration, a higher proportion of salmon chose the northern route (Putman et al. 2013). These findings provided evidence for geomagnetic imprinting in salmon, yet other environmental factors, notably sea surface temperature, also accounted for a considerable portion of the variation in return routes, consistent with previous studies (Quinn and Groot 1987). In a subsequent study with both sockeye and pink salmon, however, variations in the local magnetic field near the Fraser River accounted for more of the variation in return route for both species than did sea surface temperature (Putman et al. 2014a). These results,

combined with recent findings in sea turtles and sea birds, provide strong empirical evidence for geomagnetic imprinting and suggest that this process may underlie long-distance natal homing in diverse animals (Putman et al. 2013; Brothers and Lohmann 2015, 2018; Lohmann and Lohmann 2019; Wynn et al. 2020).

Yet another use of magnetic cues by salmon occurs when young salmon fry first emerge from gravel and enter the water column (Putman et al. 2018). Chinook salmon (*Oncorhynchus tshawytscha*) ready to emerge were placed in vertical tubes filled with transparent substrate that replicated conditions within a nest while allowing observations of the fish. Fish were exposed to one of three magnetic field conditions: (1) the ambient magnetic field; (2) an 'intensified' field in which the strength of the vertical component was increased; and (3) a magnetic field in which the normal vertical component was inverted (Fig. 4a). Fish tested in the normal ambient field moved upward significantly farther than did fish exposed to the inverted magnetic field condition (Fig. 4b). By contrast, fish tested in the intensified magnetic field moved upwards only slightly, with the mean distance falling between the means of the other two groups. These results are consistent with the interpretation that the magnetic field is one of several factors that influences emergence from the gravel, possibly serving as an orientation cue that helps fish determine which way is up.

Eels (Anguillidae)

In contrast to salmon, eels are catadromous, meaning they hatch in the ocean and migrate to freshwater (or brackish water) habitats where they feed until the onset of sexual maturity, after which they return to the ocean and migrate back to their natal area to reproduce. In contrast to salmon, most eels are panmictic; in other words, they comprise a single, randomly breeding population, with the larvae apparently transported to coastal areas largely by ocean currents (Aoyama 2009).

In an early study (Branover et al. 1971), adult European eels (*Anguilla anguilla*) were placed in an experimental arena and exposed to magnetic fields generated by an electromagnet. In the local magnetic field of the test site (Kaliningrad, Russia), eels showed bimodal orientation, but this orientation became random when eels were exposed to the imposed magnetic field. Several additional studies conducted during the same decade also demonstrated behavioral responses of eels to electromagnetic cues (McCleave et al. 1971; Rommel and McCleave 1973; Tesch and Lelek 1973; Tesch 1974), although responses were variable and sometimes difficult to interpret. With hindsight, the magnetic fields used in these early experiments were often unnatural and sometimes several orders of magnitude stronger than

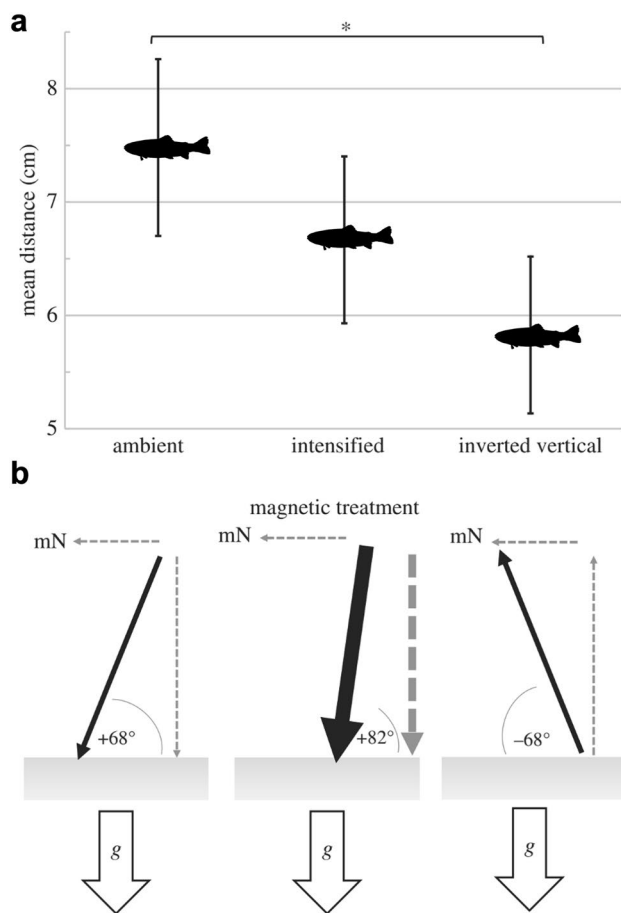


Fig. 4 **a** Mean height of fish movement under three different magnetic field conditions. Asterix denotes significance at $p < 0.05$. **b** The features of each magnetic field. Horizontal and vertical components of the geomagnetic field are grey dashed arrows and ‘mN’ denotes magnetic north. The solid black arrow denotes the direction of the resultant field, with greater width indicating increased field intensity. White arrows at the bottom indicate the direction of the gravity vector (Modified from Putman et al. 2018)

Earth’s magnetic field, which may have contributed to inconsistent results (Wiltshcko and Wiltshcko 1995). Nonetheless, these studies provided initial evidence for a magnetic sense in eels and laid the foundation for future studies of fish magnetoreception.

Subsequent studies using more natural magnetic fields have confirmed that at least three species of anguillid eels are capable of magnetoreception (Table 1). In a study involving European eels at the resident yellow eel stage (Durif et al. 2013), eels tested in a funnel-shaped tank used directional information from Earth’s magnetic field to guide their escape behavior, which took the form of brief movements up the sides of the funnel. The direction that the eels moved depended on the direction they were displaced from their holding tanks. This same magnetic compass response changed with ambient temperature; eels tested at lower

temperatures exhibited unimodal orientation approximately perpendicular to the direction they were displaced, while individuals tested at higher temperatures exhibited bimodal orientation. The authors propose that temperature might influence the eels’ motivation (e.g., whether they are sedentary or migratory).

During the spring, jelly-like glass eels enter estuarine environments, often in huge biomass. Unlike the open-sea migratory stages (e.g., eel leptocephali larvae and adult silver eels), glass eels are easily obtained by researchers. For this reason, glass eels have been the focus of many sensory studies, including some involving magnetoreception. In one study (Cresci et al. 2017b), laboratory experiments were combined with in situ behavioral observations. Glass eels tested in the laboratory under a series of rotated magnetic fields swam north during flood tides and south during ebb tides. By contrast, eels tested in floating arenas in the ocean did not differ in orientation between the different tides. Why the laboratory results and in situ results differed is not known, but one possibility is that glass eels in the ocean were influenced by sensory cues that were not present in the lab. Regardless, the laboratory results demonstrate that glass eels possess a magnetic compass sense, which might be linked in some way to the tidal cycle. Precedents for linkages between biological rhythms and orientation and/or swimming behavior exist (Cronin and Forward 1979; Lohmann and Willows 1987; Zhang et al. 2013). Further studies with glass eels are likely to be enlightening.

Although eels clearly have a magnetic compass, it is unlikely that the oceanic migrations undertaken by eels can be accomplished with a compass sense alone. Recent studies have revealed that young eels also exploit positional information in Earth’s magnetic field and thus have a kind of magnetic map (Naisbett-Jones et al. 2017). European eels hatch in the Sargasso Sea and travel across the Atlantic Ocean to freshwater growth habitats along the coasts of Europe and North Africa, where they mature (Tesch 2003). To investigate whether young eels have a magnetic map sense, glass eels were subjected to magnetic fields replicating those found at several locations along the eel’s migratory route (Naisbett-Jones et al. 2017). Eels tested in a magnetic field like one that exists near their spawning area swam southwest. Those exposed to a field that exists further along the migratory route and closer to Europe swam northeast. Simulations carried out with an ocean circulation model revealed that swimming in the experimentally observed directions at the locations where the fields exist would result in increased entrainment in the Gulf Stream System, the oceanic current system that facilitates transport of young eels to European growth habitats. Thus, the results imply that young eels possess a magnetic map sense which can be used to distinguish among magnetic fields that exist in different oceanic regions; different magnetic fields along the migratory

route elicit changes in swimming direction that presumably facilitate transport to appropriate destinations.

Numerous questions remain, however, about the eels' magnetic map; studies are challenging, in part, because working with key life-history stages is difficult. For example, eel larvae (leptocephali) rarely survive in captivity and their behavior is nearly impossible to observe in the wild. Although adult eels can be obtained, eliciting consistent orientation responses from them has proven difficult (Karlsson 1985). While it seems likely that the magnetic map sense of young eels is retained throughout life and is used by adults during the spawning migration (Putman et al. 2017), this remains to be determined.

Magnetic sense in other bony fish

Although salmon and eels are the fishes that have been studied most extensively in the context of magnetoreception, magnetic field detection has also been demonstrated in a growing number of other bony fishes, primarily through conditioning techniques, orientation studies, or both (Table 1). One of the first studies to use magnetic conditioning techniques on a fish was carried out with juvenile yellowfin tuna (*Thunnus albacares*), which were trained in water-filled arenas surrounded by a wire coil that could be used to alter the ambient magnetic field (Walker 1984). Fish were conditioned to swim through a rectangular pipe frame. Some individuals received a food reward for passing through the frame when the ambient magnetic field was altered, while others were rewarded for passing through the frame when the ambient field was unchanged. Fish quickly learned to discriminate between the two magnetic field conditions, although the exact parameter(s) of the field detected by the fish could not be determined. A similar approach was later used in studies with several additional species (e.g., Walker et al. 1997; Newton and Kajiura 2020a), demonstrating that magnetic conditioning is viable in diverse fishes. A somewhat different technique involving cardiac conditioning has provided evidence that rainbow trout can detect not only changes in magnetic field direction, but also large shifts in magnetic field inclination and intensity (Hellinger and Hoffmann 2009).

Captive zebrafish (*Danio rerio*) have also been conditioned to respond to imposed magnetic fields (Shcherbakov et al. 2005). Fish were placed in a tank and trained to swim to the opposite side when the field intensity was increased with magnetic coils. The behavior was reinforced by exposing fish that made the incorrect choice to weak electrical discharges. Interestingly, although zebrafish learned to discriminate between the different magnetic fields, they did not perform as well as migratory fish (Mozambique tilapia;

Oreochromis mossambicus) trained and tested in the same apparatus (Shcherbakov et al. 2005).

Evidence for magnetoreception in zebrafish has also been acquired in orientation studies in which the horizontal and/or vertical components of the ambient field were altered (Takebe et al. 2012; Osipova et al. 2016; Krylov et al. 2016). Although inconsistencies exist among results from the different studies, one peculiar pattern that emerged repeatedly was a tendency of zebrafish to exhibit bimodal (or axial) orientation (Takebe et al. 2012; Osipova et al. 2016; Krylov et al. 2016). The alignment of this bimodal response appeared to shift in response to changes in the direction of the horizontal field. Details remain to be resolved, but the overall results are consistent with the interpretation that zebrafish have a magnetic compass. Little is known about how magnetic cues are exploited by zebrafish, though some evidence suggests that magnetic field information might be used to orient rheotactic behavior when fish are part of shoals (Cresci et al. 2017a, 2018). Given that zebrafish are a genetic model organism, they represent a promising system for elucidating the mechanism(s) and genetic basis of magnetoreception.

Coral-reef fishes are another piscine group capable of magnetoreception. After hatching, coral-reef fish larvae often disperse tens of kilometers away from their natal reefs; then, after days to weeks in the open ocean, many return to their home reef and settle there (Brothers et al. 1983; Gerlach et al. 2007). Previous studies have suggested that olfactory cues play a role in helping larvae locate their reef once they are close (Gerlach et al. 2007), but the mechanism underlying the initial stages of this migration have only recently been studied. Cardinal fish (*Ostorhinchus doederleini*) collected shortly after settlement on a reef in Australia were tested for a magnetic compass sense (Bottesch et al. 2016). Fish tested under ambient magnetic field conditions during the day and night oriented southeast, a direction that may help the fish reach the home reef after currents displace them to the north and west (Fig. 5). To investigate whether a magnetic compass plays a role in this orientation, a group of fish was tested at night in a magnetic field in which the horizontal component was rotated 120° clockwise. These fish showed a corresponding shift in orientation (Fig. 5). The results suggest that a magnetic compass sense guides the night-time swimming behavior of larval reef fish. Additional studies on damselfish (*Chromis atripectoralis*), another coral-reef species, have demonstrated that a magnetic compass sense is present in pre-settlement larvae and is used during daytime navigation (O'Connor and Muheim 2017). The results, thus, suggest that a magnetic compass helps guide movements in several reef fishes.

In addition to the species and groups already discussed, evidence for magnetoreception also exists in a number of other bony fishes (Table 1), including tilapia (*Oreochromis*

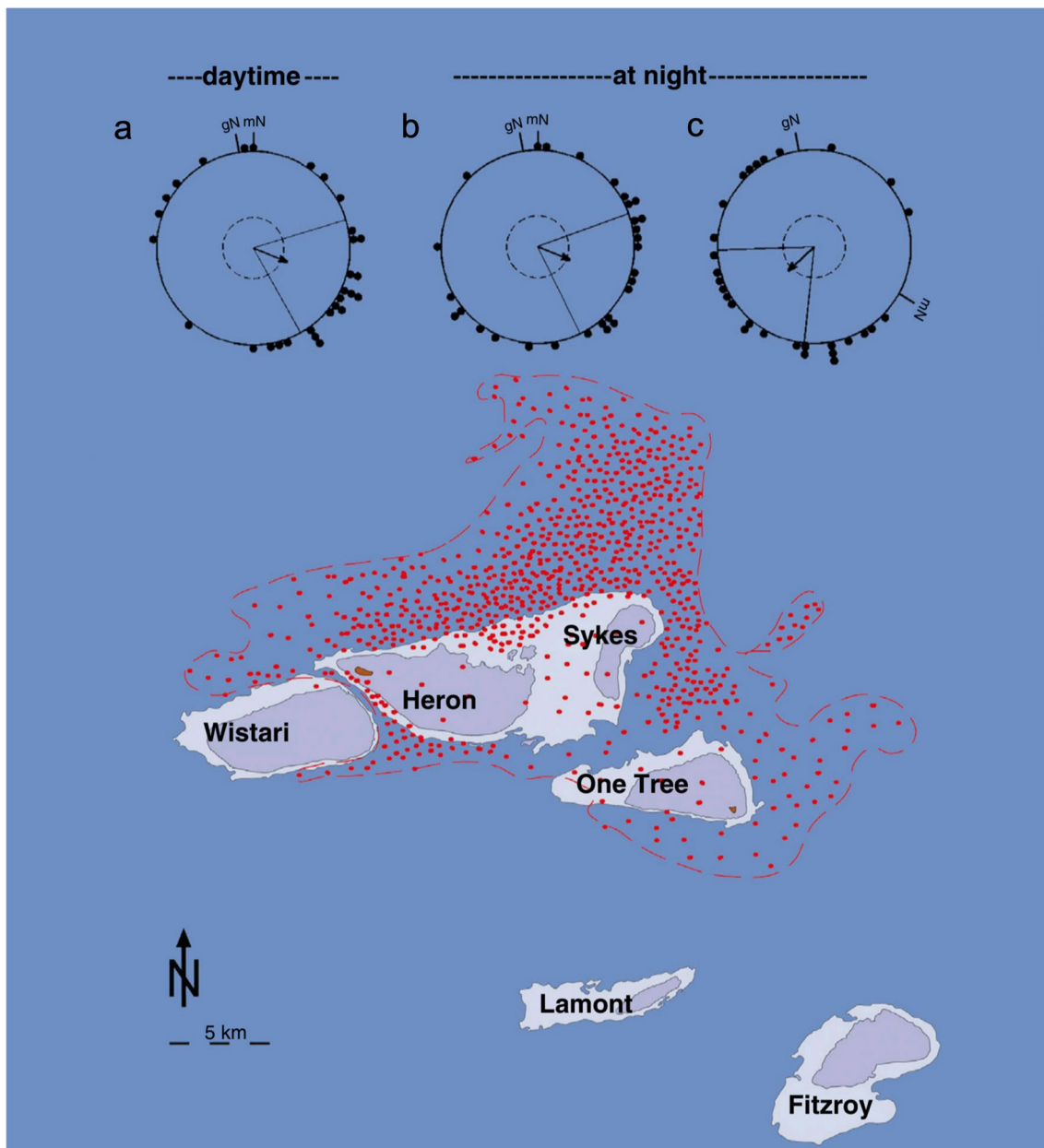


Fig. 5 Map of Capricorn Bunker Reef Group, Australia, and results of orientation experiments. Red dots indicate the expected distribution of passively dispersing particles released from One Tree Reef (see Bottesch et al. 2016 for details of hydrodynamic model). Purple patches indicate lagoons and white patches indicate reef slopes where the depth reaches 20 m. Circular diagrams at the top of the figure indicate the orientation of fish tested: **A** under clear skies and natural magnetic field conditions during the day; **B** under natural magnetic field conditions at night; and **C** at night in a magnetic field in which

the horizontal component was rotated 120° clockwise. For each diagram, ‘mN’ indicates magnetic North and ‘gN’ indicates geographic North. Each black dot represents the mean direction of a single fish. Arrows within each circle indicate the mean direction of the group. Lines on either side of the arrows indicate the 95% confidence intervals for the mean angle. Dashed circles indicate the radius needed to achieve significance ($p < 0.05$) based on the Rayleigh test. Figure is modified from Bottesch et al. (2016)

mossambicus) (Shcherbakov et al. 2005), roach (*Rutilus rutilus*) (Krylov et al. 2016), haddock (*Melanogrammus aeglefinus*) (Cresci et al. 2019b) and medaka (*Oryzias latipes*) (Myklatun et al. 2018). These findings imply that the ability

to detect magnetic fields is widespread among bony fishes and perhaps even universal.

Cartilaginous fishes

Investigations into the magnetic sense of chondrichthyan fishes have so far focused exclusively on sharks, skates, and rays from the subclass Elasmobranchii (Table 2). These ancient marine fishes possess an extremely sensitive electrical sense that allows them to cue in on the bioelectric fields of their prey (Kalmijn 1966, 1971). In principle, this same sense might indirectly provide the physical basis of a magnetic sense (Kalmijn 1973, 1982), although whether it does remains unknown (Johnsen and Lohmann 2005, 2008).

The first evidence for magnetic field detection in elasmobranchs came from behavioral studies on leopard sharks (*Triakis semifasciata*) (Kalmijn 1978). Observations of captive sharks revealed that each morning they tended to rest in a part of the tank that corresponded with magnetic north. Occlusion of visual cues had no effect on this behavior and relocating the tanks to a new location failed to disrupt it.

By contrast, using a magnetic coil system to null Earth's magnetic field within the tank led to random dispersal of the fish, suggesting that they were using magnetic cues to orient. Magnetic conditioning techniques were subsequently used to investigate whether the round stingray (*Urolophus halleri*) can perceive magnetic fields (Kalmijn 1978). Two individuals were trained to feed on the eastern side of their enclosure, with a magnetic coil system being used to reverse the field in half of the trials. The stingrays soon learned to move toward the side of the arena that corresponded to magnetic east under both magnetic field conditions, providing additional evidence for magnetic sensitivity in elasmobranchs.

Since this early work, a number of additional behavioral studies have provided experimental evidence consistent with the hypothesis that elasmobranchs possess a magnetic sense. Yet the presence of a highly sensitive electric sense in elasmobranchs greatly complicates interpretation of results of experiments involving magnetic fields. The central difficulty is that changing a magnetic field, as is normally done in magnetoreception research, also unavoidably generates

Table 2 Experimentally demonstrated behavioral responses of cartilaginous fishes to electromagnetic stimuli

Class	Order	Family	Species	Citations	Types of responses
Chondrichthyes	Myliobatiformes	<i>Urotrygonidae</i>	<i>U. jamaicensis</i>	(Newton and Kajiura 2017, 2020a, b)	Conditioning, compass, Anomalous
"	"	"	<i>U. halleri</i>	(Kalmijn 1978)	Conditioning
"	"	<i>Dasyatidae</i>	<i>D. americanus</i>	(O'Connell et al. 2010, 2011b)	Anomalous
"	Rajiformes	<i>Rajidae</i>	<i>R. clavata</i>	(Smith and O'Connell 2014)	Anomalous
"	Carcharhiniformes	<i>Carcharhinidae</i>	<i>C. plumbeus</i>	(Meyer et al. 2005; Siegenthaler et al. 2016; Anderson et al. 2017)	Conditioning, anomalous
"	"	"	<i>C. leucas</i>	(O'Connell et al. 2014c)	Anomalous
"	"	"	<i>N. brevirostris</i>	(O'Connell et al. 2011a, 2014a)	Anomalous
"	"	"	<i>R. terraenovae</i>	(O'Connell et al. 2011b)	Anomalous
"	"	"	<i>C. limbatus</i>	(O'Connell et al. 2011b)	Anomalous
"	"	"	<i>C. tilstoni</i>	(Rigg et al. 2009)	Anomalous
"	"	"	<i>C. amblyrhynchos</i>	(Rigg et al. 2009)	Anomalous
"	"	"	<i>R. acutus</i>	(Rigg et al. 2009)	Anomalous
"	"	"	<i>G. glyphis</i>	(Rigg et al. 2009)	Anomalous
"	"	<i>Sphyrnidae</i>	<i>S. mokarran</i>	(O'Connell et al. 2015)	Anomalous
"	"	"	<i>S. lewini</i>	(Klimley 1993; Rigg et al. 2009)	Anomalous, other
"	"	"	<i>S. tiburo</i>	(Keller et al. 2021)	Map
"	"	<i>Scyliorhinidae</i>	<i>S. canicula</i>	(Smith and O'Connell 2014)	Anomalous
"	"	<i>Triakidae</i>	<i>M. canis</i>	(O'Connell et al. 2011b)	Anomalous
"	"	"	<i>T. semifasciata</i>	(Kalmijn 1978)	Alignment
"	Squaliformes	<i>Squalidae</i>	<i>S. acanthias</i>	(O'Connell et al. 2014b)	Anomalous
"	Orectolobiformes	<i>Ginglymostomatidae</i>	<i>G. cirratum</i>	(O'Connell et al. 2010)	Anomalous

Compass = evidence that fishes use directional information in Earth's magnetic field; map = evidence that fishes use positional information in Earth's magnetic field; alignment = studies indicating spontaneous alignment of fishes relative to the axis of magnetic field lines; anomalous = avoidance, attraction, or other responses of fishes to strong (greater than earth strength) anomalous magnetic fields produced by a magnet, solenoid, or magnetic coil; conditioning = conditioning of fishes to magnetic field stimuli; other = other evidence (not included in the previous categories) that suggests or demonstrates magnetic sensitivity.

a transient electrical field (Faraday 1832). For animals that lack an electric sense—i.e., the vast majority of species in the animal kingdom—this weak electric field is of no consequence. But for animals such as elasmobranchs that are exquisitely sensitive to electrical stimuli, disentangling whether fish are responding to magnetic or electric stimuli in a given situation is often challenging.

From an ecological perspective, there are good reasons to suspect that elasmobranchs are magnetically sensitive, inasmuch as many species undertake lengthy and highly oriented migrations across ocean environments where an ability to sense Earth's magnetic field would potentially be useful in navigation (e.g., Carey and Scharold 1990; Bonfil et al. 2005). At present, however, unequivocal demonstrations that elasmobranchs detect and exploit earth-strength magnetic fields in navigation have remained sparse, in part because of the inseparable nature of electric and magnetic fields. For example, in a laboratory conditioning experiment involving captive sandbar (*Carcharhinus plumbeus*) and hammerhead sharks (*Sphyrna lewini*), fish learned to approach an object in the center of the tank when a wire coil surrounding the tank was turned on, which increased the intensity of the magnetic field (Meyer et al. 2005). Sharks could clearly determine when the coil was turned on, yet in principle might have solved the discrimination task in one of two ways: either by detecting changes in the magnetic field, or by detecting and responding to the transient electrical fields that were produced each time the magnetic coil was activated (Johnsen and Lohmann 2005). Follow-up studies using the same conditioning technique suggested that the background electrical environment at the test site was sufficiently 'noisy' that discriminating transient electrical signals from the coil might have been difficult, consistent with the hypothesis that the sharks detected the magnetic field (Anderson et al. 2017); at the same time, measurements of the transient electrical fields revealed that they were above the threshold that sharks can detect, so that the possibility of a response to electric fields cannot be entirely excluded. These findings highlight the challenges of studying magnetoreception in electrically sensitive animals.

Despite these obstacles, several experiments have provided strong evidence for a magnetic sense in elasmobranchs. In a study with yellow stingrays (*Urobatis jamaicensis*) (Newton and Kajiura 2020a), fish were placed in a T-shaped maze and conditioned to associate either the north or south arm of the maze with a food reward. A magnetic coil was then used to alternate the direction of magnetic north or south between the two arms. Fish learned to select the correct maze arm based on the polarity of the imposed magnetic field. As with earlier conditioning experiments with round stingrays (Kalmijn 1978), the results are consistent with the interpretation that these fish have a magnetic compass sense.

Relative to teleost fishes, few studies have investigated whether elasmobranchs possess a magnetic map sense. A recent study with bonnethead sharks (*Sphyrna tiburo*), however, has provided strong evidence that sharks can indeed exploit positional information in Earth's magnetic field (Keller et al. 2021). Juvenile bonnethead sharks were captured in the Gulf of Mexico near the Florida panhandle, in a location where land prevents long-distance movements to the north. Fish were tested in three different magnetic fields: (1) the local magnetic field of the capture site; (2) a magnetic field replicating one that exists in the ocean ~600 km south of the capture site; and (3) a magnetic field that exists ~600 km north of the capture site on the US mainland. Fish tested in the local field and in the northern magnetic field condition oriented in random directions. By contrast, fish tested in the southern magnetic field condition oriented approximately northward, the direction they would need to travel to return to the capture site from the location where the southern magnetic field actually exists. Why sharks failed to respond to the northern magnetic field was unclear. An interesting possibility, however, is that sharks had no experience with fields that exist to the north because land prevented them from moving north from the capture site (Keller et al. 2021). Regardless, the results provide the strongest evidence to date of a magnetic map sense in sharks and suggest that bonnethead sharks might be a promising species for future studies.

In a related analysis, Keller et al. (2021) investigated whether the use of magnetic positional information in navigation might explain aspects of the genetic structure of bonnethead populations, as has been reported in sea turtles (Brothers and Lohmann 2018). Specifically, if sharks imprint on the magnetic field of their natal area and return to the site partly by relying on magnetic navigation, then a relationship may exist between population genetics and the magnetic fields that exist in different locations where bonnetheads reproduce (Keller et al. 2021). For example, geographic areas with similar magnetic fields may be used by genetically similar sharks because sharks have difficulty distinguishing between the two locations. To test this hypothesis, the population structure of bonnetheads was analyzed in the context of spatial variation in the earth's magnetic field. Results revealed a relationship between genetic differentiation and the magnetic fields that exist at different reproductive sites. These findings bolster the evidence for magnetic navigation in bonnetheads. In addition, they complement earlier findings with sea turtles suggesting that geomagnetic imprinting and magnetic navigation are important drivers of population structure in some migratory animals (Brothers and Lohmann 2018; Lohmann and Lohmann 2019).

Conditioning studies with yellow stingrays have also investigated whether elasmobranchs can detect parameters of Earth's magnetic field that might function in a magnetic map. Stingrays were placed in a tank and trained to move

across the central axis of the tank when the magnetic field within the tank was repeatedly changed (Newton and Kajjura 2020b). Results implied that the fish could distinguish between a field that oscillated between two inclinations and a field that oscillated between two different intensities. Two different interpretations are possible (Newton and Kajjura 2020b). One is that the stingrays can detect magnetic inclination and intensity, features of the geomagnetic field that underlie the magnetic map sense in other fishes; another is that the fish detected and responded to the two different transient electric fields generated by the different field changes. Regardless, the findings are intriguing and warrant further investigation.

To date, nearly all studies involving magnetic maps in fishes have focused on use of magnetic parameters such as inclination and intensity, which vary predictably over large oceanic regions (Fig. 1). A different form of magnetic navigation, based on fine-scale magnetic topography, has been proposed for scalloped hammerhead sharks (Klimley 1993). Night-time tracking of scalloped hammerheads revealed that fish performed highly directional movements between foraging areas and seamounts, often through areas of variable ocean currents, bathymetry, and temperature (Klimley 1993). Analysis of paths relative to the local magnetic field contours suggested that the trajectories of the shark's tracks could often be explained if sharks are attentive to local gradients in magnetic intensity associated with the seamounts. Further investigation is warranted.

A final line of evidence for magnetoreception in elasmobranchs comes from studies involving responses of sharks and rays to strong magnets. For unknown reasons, some elasmobranchs appear to spontaneously avoid magnets when they first encounter them (O'Connell et al. 2011a). In a conditioning study, however, yellow stingrays were trained to approach magnets buried in the sediment (Newton and Kajjura 2017). Although all of these findings are consistent with the interpretation that the fish can detect magnetism—either directly with a magnetic sense or indirectly with their electric sense—the relationship between detecting unnaturally strong fields under laboratory conditions, and detecting weaker natural fields in the environment, remains to be elucidated.

Mechanisms of magnetic field detection

Little is known about the mechanism or mechanisms that underlie magnetic field detection in fishes. In a group as large and diverse as fishes, it is possible that magnetoreception has evolved independently on multiple occasions, so that different mechanisms exist in different fish species. Indeed, it is even possible that at least two different mechanisms exist within the same species, with one mechanism

underlying the magnetic compass and a different mechanism involved in detecting magnetic parameters associated with a magnetic map (Lohmann 2010).

Most recent research on magnetoreception mechanisms, both in fish and in other animals, has focused on three main hypotheses (Johnsen and Lohmann 2005, 2008; Nordmann et al. 2017). The first involves crystals of biogenic magnetite coupled to mechanoreceptors. The second proposes that electrically sensitive animals such as elasmobranchs detect magnetic fields via electromagnetic induction (Kalmijn 1973), and/or that animals such as birds detect magnetic fields with an induction-based mechanism located within the semi-circular canals of the inner ear (e.g. Nimpf et al. 2019). The third hypothesis proposes a complex series of biochemical reactions that are modulated by earth-strength magnetic fields. All of these mechanisms are presently hypothetical, inasmuch as primary magnetoreceptors have not yet been identified unequivocally in any animal. Nevertheless, behavioral and histological studies have provided some initial indications about how fishes might sense magnetic fields.

For bony fishes, evidence consistent with the magnetite hypothesis has come from studies in which magnetic material (presumably magnetite) has been detected in magnetically sensitive species such as eels, salmon and tuna (Walker et al. 1984, 1988; Kirschvink et al. 1985; Ogura et al. 1992; Moore and Riley 2009). Although direct evidence that these magnetic crystals function in magnetoreception has not been acquired, efforts have been made to investigate possible links between putative magnetite-based receptors and the nervous system. For example, in a study with rainbow trout, Walker et al. (1997) used electrophysiological techniques to record from the ophthalmic branch of the trigeminal nerve while the fish were exposed to changes in the ambient magnetic field. Results provided evidence of enhanced neural activity in response to the field changes. Because the nerve branch from which the recordings were obtained innervates the nose of the fish, the results were consistent with the hypothesis that receptors for the magnetic sense in fish, and perhaps in other vertebrates, are located in or near the nasal area. In the same study, the authors identified potential magnetoreceptor cells in the olfactory lamellae; these structures were subsequently found to contain crystals of single-domain magnetite (Diebel et al. 2000). These findings are promising, yet additional studies are needed to establish a definitive link between the putative receptors and the magnetic sense, both in rainbow trout and in other fishes.

Additional evidence consistent with the magnetite hypothesis has been obtained in behavioral experiments in which animals have been exposed to strong magnetic pulses (e.g., Wiltschko et al. 2002; Holland 2010; Ernst and Lohmann 2016). Importantly, while this technique is capable of

permanently altering the magnetic dipole moment of magnetite crystals, it should have no lasting effect on other proposed mechanisms of magnetic field detection (Shaw et al. 2015). Thus, magnetic pulses have been viewed by some as a behavioral diagnostic technique for magnetite-based magnetoreception (Kirschvink et al. 2001), although others have urged caution in interpreting results, given that such pulses appear to elicit at least some changes in gene expression unrelated to magnetoreception (Fitak et al. 2017; Ernst et al. 2020).

In one study (Naisbett-Jones et al. 2020), juvenile Chinook salmon were exposed to a strong magnetic pulse, after which magnetic orientation behavior of the fish was compared to that of control fish under two magnetic field conditions: (1) the local magnetic field and (2) a magnetic field that exists near the southern boundary of the fish's range. In the local field, no differences were detected between pulsed and control groups. Interestingly, however, the orientation of the two groups was significantly different when tested in the magnetic field from the distant location. It is unclear whether the magnetic pulse affected the magnetic compass, map sense, or both, but the results are consistent with the hypothesis that at least part of a salmon's magnetoreception system is based on magnetite-based receptors. Analyses of gene expression in rainbow trout after exposure to a similar magnetic pulse revealed that 181 genes had altered expression (Fitak et al. 2017). Some were ferritin genes involved in the binding and trafficking of iron and might, in principle, function to repair or replace magnetite-based magnetoreceptors damaged by the pulse. Surprisingly, the technique of testing the effect of magnetic pulses on fish has only been used with species from the family *Salmonidae* (Fitak et al. 2017, 2020; Arniella et al. 2018; Naisbett-Jones et al. 2020). Thus, whether other fishes are also affected by a magnetic pulse remains unclear.

Magnetite is not the only mechanism that has been proposed to underlie magnetoreception in fishes. For species capable of electroreception, an alternative possibility is electromagnetic induction. Distilled to its simplest form, the electromagnetic induction hypothesis proposes that fish capable of electroreception use their electrical sense to sense magnetic fields indirectly. Specifically, as elasmobranchs such as sharks swim through Earth's magnetic field, a slight separation of charge presumably develops between the dorsal and ventral surfaces of the fish; the fish might then use their highly sensitive electroreceptors to detect the voltage drop of the induced current that flows through the sea water around them (Kalmijn 1973; Johnsen and Lohmann 2008).

Whether elasmobranchs actually perceive magnetic fields in this way, however, is not known. Moreover, distinguishing between the magnetite hypothesis and the electromagnetic induction hypothesis has proven challenging. In principle, a critical test might involve attaching magnets to fish. If

the magnet is stationary relative to electroreceptors, then it should not affect a mechanism based on induction, but it should affect a mechanism based on magnetite (Johnsen and Lohmann 2005).

Following this rationale, Walker et al. (2003) sought to test whether magnetoreception in short-tailed stingrays (*Dasyatis brevicaudata*) is based on magnetite or electromagnetic induction. Stingrays were first trained to discriminate between the presence and absence of a magnetic anomaly produced by a coil system. Next, small neodymium magnets or non-magnetic brass bars were implanted into the nasal cavity of the rays. Fish from the control group with the brass bars were able to successfully discriminate between the anomalies, but those with magnets were unable to do so. Similar results were subsequently obtained in experiments with sandbar sharks (Anderson et al. 2017). In both cases, the results were interpreted as evidence for a magnetite-based mechanism. A crucial question in all such tests, however, is whether the movements of the magnets precisely matched the movements of electroreceptors on the flexible bodies of the fish; if slight differences in motion occurred, then a magnetoreception system based on induction might inadvertently have been affected (Johnsen and Lohmann 2005). Indeed, studies modelling the movement of the fish's bodies relative to the attached magnets suggest that the movement of the magnet might have been sufficient to impair an induction-based mechanism (Molteno and Kennedy 2009). Future experiments with weaker magnets that are less likely to interfere with an induction-based mechanism may help elucidate the mechanism of magnetoreception in elasmobranchs (Molteno and Kennedy 2009). For now, the question remains unresolved.

An additional mechanism that has been proposed to underlie magnetic field detection involves a complex series of chemical reactions that may involve photopigments known as cryptochromes (Ritz et al. 2000). Although evidence consistent with this hypothesis has been acquired in some animals, especially in insects and birds (e.g., Ritz et al. 2004; Gegear et al. 2008; Wan et al. 2021; Netušil et al. 2021), the idea has received little attention in fishes. Nonetheless, studies with zebrafish have revealed the presence of cryptochromes without a known function, leading to the suggestion that these play a role in magnetoreception (Balay et al. 2020). Further study is needed to investigate this hypothesis.

Given the potential involvement of photopigments in magnetic field detection, the finding that magnetic orientation behavior in some animals is light-dependent, and also that it is affected by specific wavelengths of light, has been interpreted as support for the chemical magnetoreception hypothesis (e.g., Phillips and Borland 1992; Wiltschko and Wiltschko 1999). Few studies have investigated the relationship between light and magnetoreception in fishes, although

some evidence suggests that salmonids can detect magnetic stimuli in total darkness (Quinn 1980; Hellinger and Hoffmann 2012), suggesting that magnetoreception in this group might occur independent of light. Whether this is a universal feature of magnetoreception in fishes remains to be explored.

Missing behavioral links in fishes

The existence of a magnetic sense in diverse groups of fishes suggests that magnetoreception has either been heavily conserved through evolution or has evolved independently in multiple groups. The astonishing diversity of fishes, and their evolutionary position relative to other vertebrates, provides a unique opportunity to investigate the origins and evolution of magnetoreception. Although such investigations are currently impeded by the dearth of information on magnetoreception mechanisms, useful insights can potentially be gained from behavioral experiments. For example, one of the most significant knowledge gaps exists in the ancient lineage of jawless fishes from the superclass Agnatha (Fig. 6). Two orders of agnathans, lampreys (Petromyzontidae) and hagfish (Myxiniiformes), are among the oldest existing vertebrates, having originated more than 500 million years ago (Volf 2005). Hagfish pose a challenging study system because they occupy deep benthic areas of the ocean and are difficult to acquire. Lampreys, on the other hand, are relatively common in aquatic ecosystems worldwide and represent an interesting candidate given the migratory life histories of some species (Beamish 1979). Other knowledge gaps can be found in the lobe-finned fishes from the class Sarcopterygii. Extant members from this group include members of the lungfish order (Dipnoi), as well as the coelacanth (Coelacanthiformes). While coelacanth live in deep water and are difficult to acquire, lungfish are relatively common in shallow, freshwater ecosystems worldwide and can, thus, be readily collected. Lastly, within the Chondrichthyes there are two extant subclasses of cartilaginous fishes which represent the earliest stage in the evolution of the jawed vertebrates: the Elasmobranchii (sharks, rays and skates) and the Holocephali (chimaerids and elephant sharks). To our knowledge, no study has investigated magnetoreception in Holocephali fishes. In fact, very little information exists about the sensory ecology of this group.

Future directions

Over the last half century, a wealth of behavioral evidence has demonstrated that fishes can sense Earth's magnetic field and use it to guide their movements. This ability is not

limited to iconic, long-distance migrants such as salmon and eels, but instead appears to be phylogenetically widespread. Magnetic compasses are common among fishes and exist both in species that move over short distances and those that undertake transoceanic migrations. Magnetic maps have now been discovered in several groups of fishes including salmonids, European eels, and bonnethead sharks. In addition, growing evidence suggests that such maps, in combination with geomagnetic imprinting, assist some fish in returning to natal areas to reproduce.

Despite considerable progress in recent years, research on magnetoreception in fishes is still in its infancy. Numerous questions remain unresolved, including the mechanism(s) of magnetoreception, how fish use magnetic cues in their natural behavior, and how magnetic information is integrated with other sensory systems during migration. Indeed, even a baseline knowledge of which fishes are capable of magnetoreception has not yet been acquired, insofar as studies have not been carried out with a number of key taxonomic groups.

Magnetoreception is of interest not only from the perspective of basic research, but also from the standpoint of conservation and management. Although researchers have investigated how numerous factors affect fish stocks, little consideration has been given to the electromagnetic environment. Yet nowadays aquatic environments are increasingly awash in electromagnetic fields of anthropogenic origin, generated by sources as diverse as hydroelectric and hydrokinetic facilities, underwater electrical cables, oil platforms, shipboard radar, and coastal cell phone towers. Understanding the role of magnetic fields in the lives of marine animals, and the impacts of anthropogenic fields on their welfare, is an important area for future study (Albert et al. 2020; Klimley et al. 2021).

Finally, as the oldest and most diverse vertebrate group on the planet, fishes represent a particularly promising group for studies on magnetoreception and its evolutionary origins. Many species are relatively easy to acquire and maintain in captivity, making them amenable to laboratory studies. In addition, the existence of fish model systems such as zebrafish and medaka (e.g., Lin et al. 2016; Teame et al. 2019; Hilgers and Schwarzer 2019) mean that a variety of modern genetic, molecular, and developmental approaches are feasible. Given these advantages, it appears likely that fishes will play a pivotal role in unravelling many long-standing mysteries of magnetoreception.

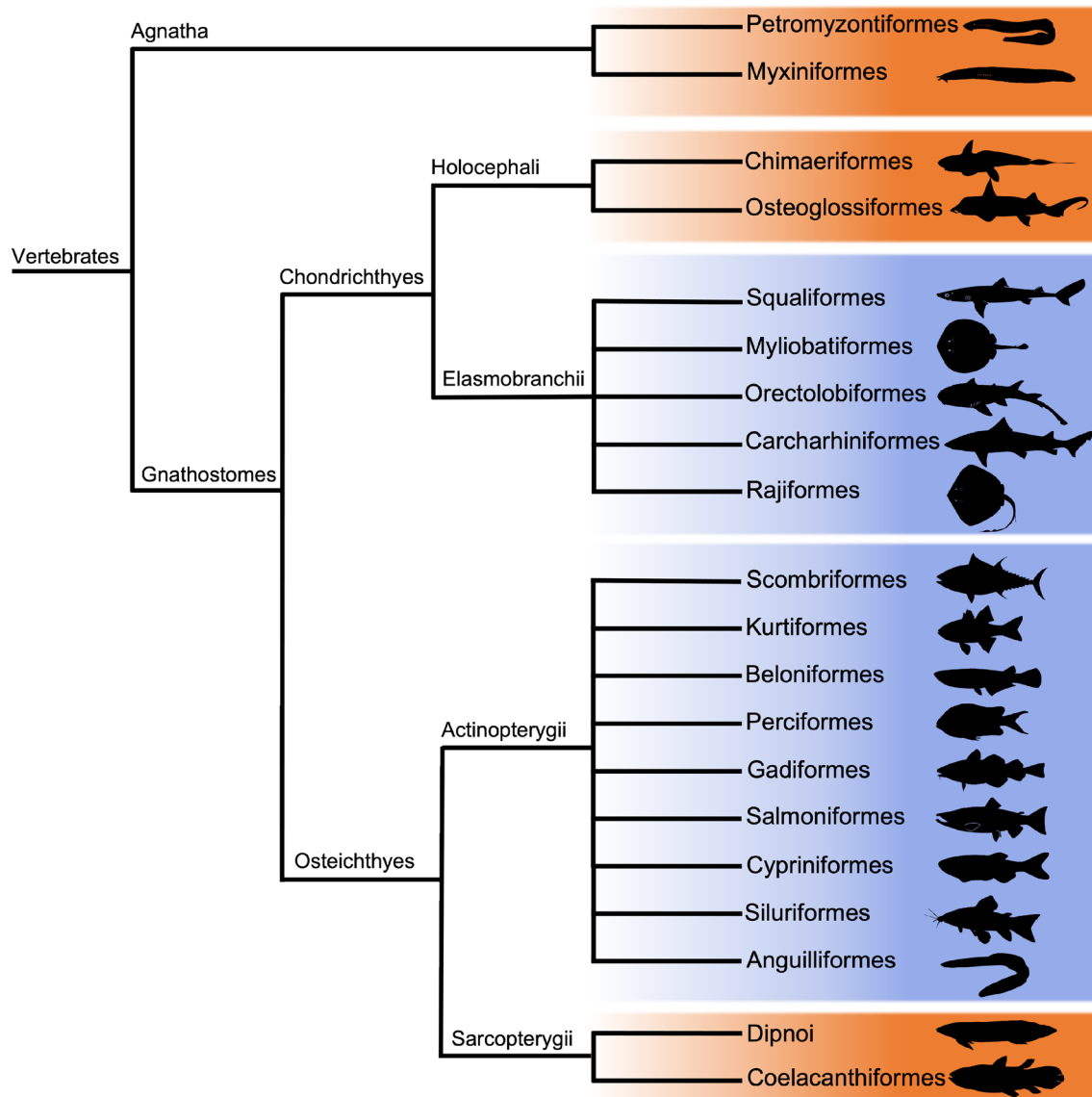


Fig. 6 A cladogram showing simplified phylogenetic relationships among the main fish groups. Clades highlighted in blue represent orders in which behavioral evidence for magnetoreception has been obtained; clades highlighted in orange show orders in which studies

of magnetoreception have not, to our knowledge, been undertaken. Silhouette images were obtained under Public Domain courtesy of PhyloPic (<http://phylopic.org>)

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Declarations

Conflict of interest The author declares that there is no conflict of interest.

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